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REVIEW ARTICLE

Effects of gaps on regeneration of woody plants: a meta-analysis

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Abstract: Forest gaps, openings in the canopy caused by death of one or more trees, have a profound effect on forest regeneration and drive the forest growth cycle. It is therefore necessary to understand the effects of forest gaps on regeneration for modern forest management. In order to provide a quantitative assessment of the effects of forest gaps on regeneration of woody plants, we conducted this review of gap effects on woody plant regeneration on the basis of 527 observations from 42 individual papers, and reported the results of these data in a meta-analysis. Overall, densities of regenerated woody plants were significantly greater (359%) in forest gaps than on the closed-canopy forest floor. The regeneration density in gaps of plantation forests was significantly greater ($P < 0.05$) than that of natural forest because the regeneration in gaps of plantation forests was improved by both gap effects and experimental measures. Similarly, in comparison to natural gaps, regeneration was better enhanced in artificial gaps. Regeneration density exhibited a significantly positive correlation with gap size, but a negative correlation with gap age because the gap size decreased with increasing gap age. Shade tolerance of woody plants affected regeneration density in gaps and understory. Average regeneration density of shade-tolerant species exhibited a significantly positive response to gaps but densities remained lower in total than those of intermediate and shade-intolerant species. Gap effects on regeneration decreased in response to increasing temperature and precipitation because of the limiting effects of lower temperature and moisture on woody plant regeneration. In summary, forest gaps enhance woody plant regeneration, and the effects of gaps varied by forest type, gap characteristics, environmental factors and plant traits. The results of this meta-analysis are useful for better understanding the effects and roles of gaps on forest regeneration and forest management.

Keywords: forest gap, regeneration, disturbance, gap size, gap age, shade tolerance

Introduction

Forest gaps, also called treefall gaps, are the openings in the forest canopy caused by the death of one or more trees (Brokaw 1982; Runkle 1982; Whitmore 1989). Gap disturbance, the basis of the “forest growth cycle” (Whitmore 1989) or “gap theory” (Yamamoto 1992), is a dominant form of small-scale disturbance. As forest managers gained understanding of forest development, silvicultural systems have changed from traditional cutting regimes oriented toward timber production to optimize harvest yields following natural forest succession (Long 2009; Wang and Liu 2011). For example, nature-based silviculture policy (Nuske et al. 2009) or close-to-nature forestry (Madsen and Hahn 2008) and continuous cover forestry policy (Mason 2003), and sustainable forestry development (Lu et al. 2002) all highlight the importance of gap disturbance. Thus, simulating gap disturbance or relying on gap disturbance has gradually become an important technology used in modern forest management (Schliemann and Bockheim 2011). Gap disturbance has emerged as a common theme in research on regeneration and succession in forests worldwide (Zhu et al. 2003; Leithead et al. 2012).

Many studies have focused on the relationship between regeneration of woody plants and forest gap formation. Gap formation changes stand structure by creating open space in the canopy that enable varying intensities of light to penetrate (Marthews et al. 2008), depending on gap size, gap shape, height of trees surrounding the gap and topography. Incoming light influences micro-environmental factors (Galhidy et al. 2006; Muscolo et al. 2007) such as soil moisture and nutrition (He et al. 2012), and ultimately affects tree regeneration (Lee et al. 2004). The effects

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of gaps on tree regeneration vary widely, in response to global variation in forest characteristics. For example, Garbarino et al. (2012) claimed that tree species compositions in large gaps differed from those in small gaps or in the understory in an old-growth *Fagus-Abies-Picea* forest. Nagel et al. (2010), in contrast, reported that structure and composition of tree regeneration were similar in gaps and in the understory in an old-growth *Fagus sylvatica-Abies alba* forest. Elias and Dias (2009) concluded that nearly all species benefited from forest gaps and confirmed the positive effects of gaps on tree regeneration in *Juniperus-Laurus* forests. Arevalo and Fernandez-Palacios (2007) reported that regeneration density in small gaps was similar to that below closed canopy, yet large gaps discouraged plant regeneration and showed lower density compared with closed-canopy understory.

Forest gaps have been researched for more than six decades after the report of Watt (1947). Mechanisms of gap regeneration have been investigated in numerous studies (Clarke 2004; Mizunaga 2007; Ibanez and McCarthy-Neumann 2014), and the effects of forest gaps on tree regeneration are still disputed. The ambiguity and confusion in current individual studies of the effects of forest gaps on tree regeneration might obstruct the understanding and application of gap theory to simulate gap disturbance in modern forest management practices.

Meta-analysis has been widely used with success in dealing with ecological data (Paquette et al. 2006; Duguid and Ashton 2013). The advantage of meta-analysis is its capacity for quantitative assessment that is lacking in traditional narrative or qualitative reviews that often lack sampling rigor and robust statistical methods (Johnson and Curtis 2001). We know of no quantitatively systematic analysis of the total body of reports on gap dynamics. We used meta-analysis to identify general patterns and to enhance understanding of the roles of forest gaps in woody plant regeneration at the global scale. We analyzed individual studies as components of a large body of literature to answer the following questions: (1) Compared with understory beneath closed canopies (hereafter "understory"), do forest gaps have a positive effect on woody plant regeneration? (2) Do regeneration results vary by forest type and by presence or absence of forest gaps? (3) Do the traits of woody plants themselves affect regeneration in gaps? (4) How do environmental conditions influence the effects of forest gaps?

Methods

Data collection

We reviewed literature using two electronic databases: "Web of Science" and "Google Scholar". Forest gap, canopy gap, treefall gap, gap dynamics, regenerate, regeneration, recruit, and recruitment were used as keywords in the search processes. There were many relevant papers, but we only reviewed studies that evaluated a paired sample (gap vs. understory) in our analysis. Many studies were excluded because they lacked pretreatment or control plot (understory) data. Moreover, only final values were extracted when studies reported repetition of sampling over time. In total, we used 42 individual publications (Table S1---Electronic supplementary material) that reported 527 observations from 1996 to 2014 to build our database. Twenty-one variables were quantified in relation to gap and understory regeneration (Table S2---Electronic supplementary material).

For each study, regeneration density of paired samples (gap vs. understory) was extracted from tables or texts directly, or from figures in original papers by the data thief software GetData Graph Digitizer 2.24 (http://getdata-graph-digitizer.com). Units of regeneration density were standardized as stems m^{-2} although the original papers reported stems per ha, stems per 100 m^2, or stems per m^2. Information on forest types, gap characteristics, and regenerated woody plant species were also collected in as much detail as possible. Forest types were classified by their formation (natural vs. plantation), and by the composition of tree species (coniferous, coniferous-broadleaved mixed, and broadleaved) (Table 1). Functional types of regenerated woody plants were identified by shade tolerance (tolerant, intermediate, and intolerant), leaf morphological traits (evergreen coniferous, evergreen broadleaved, and deciduous broadleaved) and growing stages (seedling vs. sapling), respectively (Table 1). Gaps were grouped by their formation (natural vs. artificial), gap definition (canopy gap vs. expanded gap) (The definitions canopy gap and expanded gap were defined in Table 1 as footnotes), and gap characteristics (gap size and gap age) (Table 1), wherein the upper limit of gap size was set as 1000 m^2 as recommended by Yamamoto (1992) and Schliemann and Bockheim (2011).

We determined the shade tolerance of more than 150 regenerating woody plant species by referring to the web site Ecological Society of America (http://www.esapubs.org/), and Google (http://scholar.google.com/). We compiled environmental data (Table 1), including mean annual temperature (MAT) and mean annual precipitation (MAP) from Surface meteorology and Solar Energy, a renewable energy resource web site (https://eosweb.larc.nasa.gov/) sponsored by NASA, USA. In addition, the geographic coordinates of each study were collected to produce a figure showing their geographic distribution (Fig. 1).

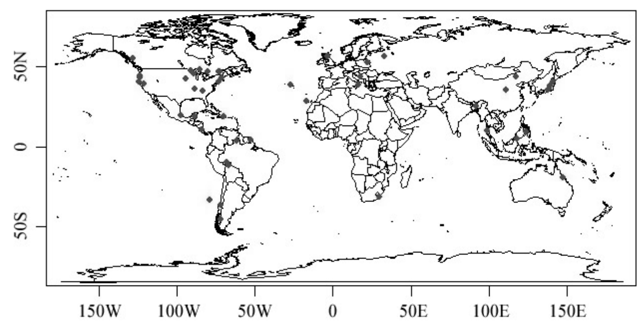

Fig. 1: Distribution of the study sites (created in R 3.0.2). **Note:** red points represent the locations of studies included in this study.

Meta-analysis

The aim of this study was to determine the mean effects of gaps on woody plant regeneration, similar to many other

meta-analyses, the response ratio (R) was employed as the effect size estimator to represent the magnitude of the gap mean relative to the control (understory) mean (Equation 1).

$$R = X_E/X_C \tag{1}$$

where X_E and X_C are the mean values (regeneration density) in the experiment (gap) and control (understory) groups, respectively (Hedges et al. 1999).

To improve statistical behavior, we used the natural log of the response ratio (R) to define the effect size estimator (Hedges et al. 1999) (Equation 2).

$$L(R) = \ln(R) = \ln(X_E) - \ln(X_C) \tag{2}$$

Some studies included zero values, i.e. no regeneration, which could not be used in computation of Equation 2. Therefore, we substituted zero values with 0.00009 to indicate regeneration density of less than 1 seedling or sapling per ha. This substitution did not affect the assumption of normality in data processing and conformed to the results of original papers as closely as possible.

Although a robust meta-analysis is preferable when studies report means, standard deviations (standard errors or confidence intervals), and the number of replicates for the experiment and control groups (Gurevitch and Hedges 1999), many studies reviewed for this analysis did not report such information. To compensate for the lack of summary statistics in some reports, we applied unweighted meta-analysis so that we could include as many studies as possible in our database (Johnson and Curtis 2001). To determine whether gaps had a significant effect on a categorical variable, we employed a randomized-effects model using MetaWin 2.1 (Rosenberg et al. 2000). The procedure is analogous to analysis of variance (ANOVA), in which the total heterogeneity (Q_T) of a group comparison is partitioned into within-group heterogeneity (Q_W) and between-group heterogeneity (Q_B) (Lin et al. 2010). We also applied a continuous model meta-analysis (Bai et al. 2013) to test whether $L(R)$ was related to continuous variables such as gap size, gap age, mean annual temperature and mean annual precipitation. Similar to its use in a categorical data model, total heterogeneity (Q_T) can be partitioned into regression model heterogeneity (Q_M) and residual error heterogeneity (Q_E). Confidence intervals (CIs) for the effect size were generated using the bootstrap procedure. If the 95% CIs for different groups did not overlap, the effects of gaps were considered to differ significantly. Where the 95% CIs did not overlap zero, the mean effects were considered significant (Lin et al. 2010).

Table 1: Regeneration differences between gaps and understory in responses to different variables.

	Variables	Q_B [f]	Q_M [g]	***P*-value**
Forest types	Natural, plantation forests	31.75		0.000
	Coniferous, coniferous-broadleaved mixed, broadleaved forests	9.49		0.009
Gap characteristics	Natural, artificial gaps	47.70		0.000
	Canopy [a], expanded [b] gaps	7.28		0.007
	Size (m^2)		6.98	0.008
	Age (year)		11.69	0.001
Functional traits	Shade tolerant, intermediate, intolerant plants	35.87		0.000
	Evergreen coniferous, evergreen broadleaved, deciduous broadleaved plants [c]	9.70		0.008
	Seedlings, saplings	0.03		0.862
Environmental factors	MAT [d] (℃)		7.16	0.007
	MAP [e] (mm)		19.95	0.000

Notes: a: the land surface area directly under the canopy opening (Runkle 1982); b: canopy gap plus the adjacent area extending to the bases of canopy trees surrounding the canopy gap (Runkle 1982); c: no deciduous coniferous species data available; d: mean annual temperature; e: mean annual precipitation; f: between-group heterogeneity for categorical variables, statistical differences were considered as significant when $p < 0.05$; g: regression model for continuous variables, relationship was considered as significant when $p < 0.05$.

Results

Gaps significantly increased the regeneration density of woody plants by 359% (with a 95% CI of 262–484%; Fig. 2) across all the studies included in our database.

Gap regeneration and forest types

Both natural and plantation forests showed significant increases in regeneration density with gap treatment. The enhancement of regeneration density with gap treatment in plantation forests (+1488%, 95% CI: 838–2587%; Fig. 2) was significantly higher (Q_B = 31.75, p <0.05; Table 1) than that in natural forests (+179%, 95% CI: 104–280%; Fig. 2). When forests were divided by composition of tree species, the positive responses of coniferous-broadleaved mixed forests (+718%, 95% CI: 417–1196%; Fig. 2) were significantly higher (Q_B = 9.49, p <0.05; Table 1) than those of broadleaved forests (+232%, 95% CI: 134–371%, Fig. 2). No significant differences were detected, however, between coniferous forests (+350%, 95% CI: 176–633%; Fig. 2) and coniferous-broadleaved mixed, or between coniferous forests and broadleaved forests (Fig. 2).

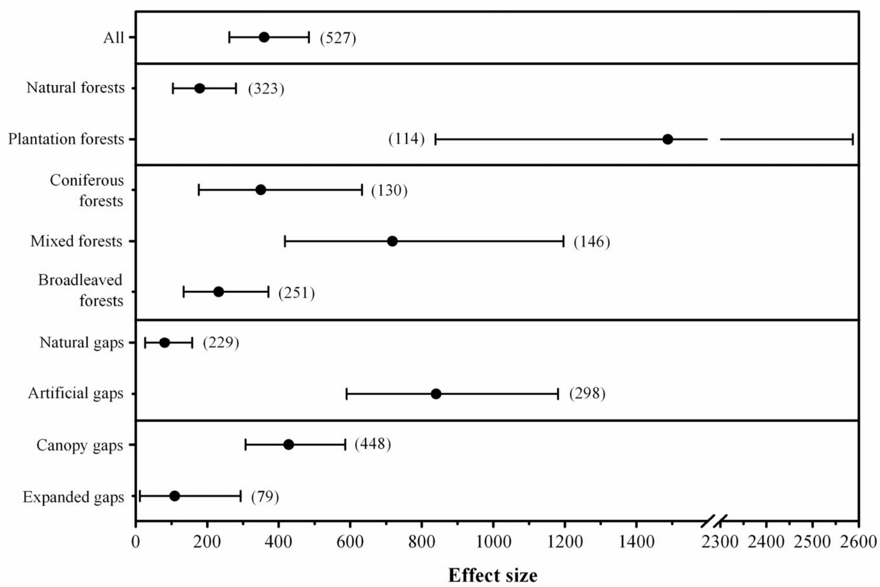

Fig. 2: Responses of regeneration density to gaps as a percent change relative to control or understory (%) for forest types and gap types. Values are means ± 95% CI. Numbers of observations are shown in parenthesis.

Gap regeneration and gap characteristics

The effect size of artificial gaps on regeneration (+840%, 95% CI: 590-1181%; Fig. 2) was significantly greater (Q_B = 47.70, P < 0.05; Table 1) than that of natural gaps (+81%, 95% CI: 27-158%; Fig. 2). Both canopy gaps (+428, 95% CI: 307-586%; Fig. 2) and expanded gaps (+109, 95% CI: 11-293%; Fig. 2) significantly enhanced the regeneration of woody plants. But the increase from canopy gaps was significantly greater (Q_B = 7.28, p <0.05; Table 1) than that from expanded gaps. The continuous randomized-effects model meta-analysis showed a significantly positive correlation between *L(R)* and gap size (r = 0.114, p <0.05; Fig. 3a, Table 1). By contrast, increased gap age had a significantly negative correlation with *L(R)* (r = -0.257, p <0.05; Fig. 3b, Table 1).

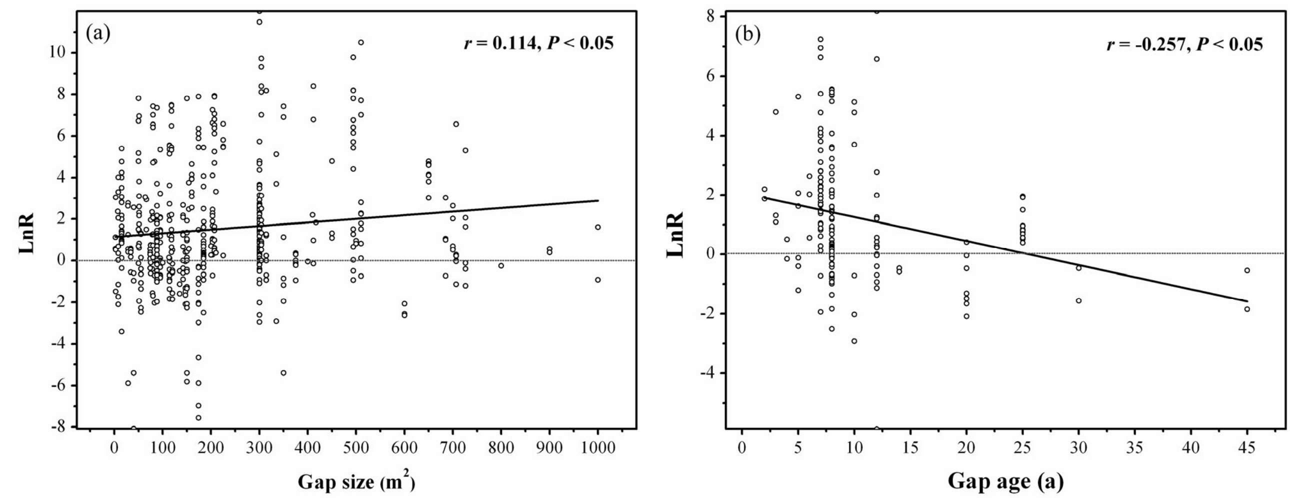

Fig. 3: The effects of gap size (numbers of observations = 527) and gap age (numbers of observations = 168) on woody plant regeneration. *Ln(R)* = 0 means no differences in plant regeneration density between gaps and understory. Regression lines, Pearson correlations (r), and significance level (P) are indicated on the figure.

Gap regeneration and plant functional types

The effects of gaps on woody plant regeneration showed a strong dependence upon some functional traits of regenerated woody plants. Gaps significantly increased the regeneration of all functional types of woody plants (Fig. 4, Table 1). The regeneration increments ranked as intolerant species (+2475%, 95% CI:

1106−5530%; Fig. 4) > intermediate species (+622%, 95% CI: 365−1023%; Fig. 4) > tolerant species (+124%, 95% CI: 48−241%; Fig. 4). Regeneration densities differed by degree of shade tolerance (Q_B = 35.87, p <0.05; Table 1). The regeneration density of deciduous broadleaved species in gaps significantly increased by 636% with a 95% CI of 415−944% (Fig. 4), which was higher (Q_B = 9.70, p <0.05; Table 1) than that of evergreen coniferous (+277%, 95% CI: 153−491%; Fig. 4) and evergreen broadleaved species (+204%, 95% CI: 89−416%; Fig. 4). Gap effect on regeneration was significant for both seedlings and saplings, but the effect did not differ by age class (Q_B = 0.03, P = 0.86; Table 1) between seedlings (+354%, 95% CI: 210−564%; Fig. 4) and saplings (+381%, 95% CI: 182−719%; Fig.4).

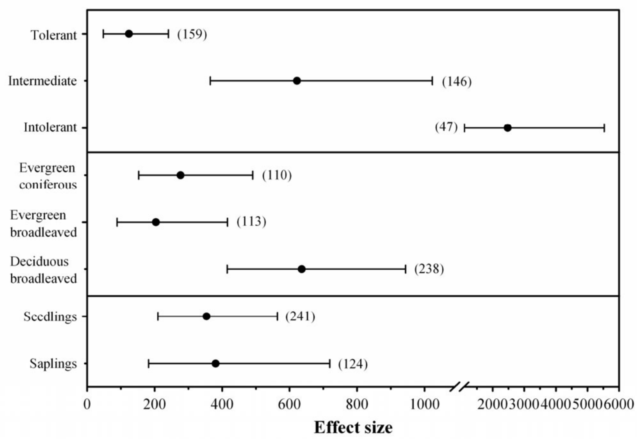

Fig. 4: Responses of regeneration density to gaps as a percent change relative to control or understory (%) for plant functional types. Values are means ± 95% CI. Numbers of observations are shown in parenthesis.

Environmental factors

We took mean annual temperature and mean annual precipitation factors into account, and found that $L(R)$ decreased as the temperature increased (r = -0.116, p <0.05; Fig. 5a, Table 1). A similar trend was found in precipitation (r = -0.191, p <0.05; Fig. 5b, Table 1).

Discussion

Overall effects of gap on woody plant regeneration

Studies, including many not entered into our database because of lack of data for paired samples (gap vs. understory), have demonstrated that gap disturbances increase densities of regenerating woody plant in various forest types (Kuuluvainen and Juntunen 1998; Hutchinson et al. 2012; Mallik et al. 2014). This was confirmed by our meta-analysis of natural forests and plantation forests and held true for coniferous, broadleaved and mixed forest types under a variety of climatic conditions and various gap categories (Table 1, Fig. 2, 3). The effects of gaps were greater for shade-intolerant woody plants but the publications we reviewed reported that these effects were significantly positive for tolerant woody plants as well (Fig. 2). On average, gaps caused a 359% increase in regeneration density (Fig. 2) from all included studies although around 30% observations reported negative responses (Table 2). The positive effects of gaps on regeneration varied according to forest types, gap characteristics, plant functional traits, and environmental factors. All categorical variables exhibited significantly positive responses on average, although some showed negative responses or no difference between gap and understory.

Effects of gap on woody plant regeneration in response to forest types

The effect size of gaps on regeneration in plantation forests were 8.3 times greater than in natural forests (Fig. 1); and >90% of observations in gaps of plantation forests were positive responses to regeneration, compared to 63% in gaps of natural forests (Table 2). These results suggested that effects of gaps on regeneration were strongly dependent on whether they were natural forests or plantation forests. The more pronounced effects of gaps in plantation forests can be attributed to three factors: (1) most gaps (90%) in plantation forests were formed artificially; (2) regeneration in gaps of plantation forests was improved by experimental treatments; and (3) 93% of the regeneration data were compiled from only three studies (Dobrowolska 2006; Wang and Liu 2011; Zhang et al. 2013) (Table S2). The less pronounced effect of gaps on regeneration in natural forests was likely because most woody plants were shade-tolerant species (78% of identified woody plants) whose regeneration was not affected by increased direct sunlight penetration in the early gap stage (Webster and Lorimer 2005; Fahey and Lorimer 2013). This result was confirmed by our meta-analysis: 37% of the observations exhibited negative (34.5%) or no (2.5%) response to the effects of gaps on regeneration (Table 2). In broadleaved forests, the positive impacts of gaps on regeneration were less pronounced because plantations and natural forests were not equally represented in field sampling (81% of studies examined natural forests and 19% plantations) (Table S2). In coniferous forests and coniferous-broadleaved mixed forests, the positive impacts of gaps on regeneration were similar but did vary depending on the proportions of observations in plantation forests versus natural forests (Fig. 2, Table S2). The greater effect of gaps on woody plant regeneration in plantation forests than in natural forests was consistent with our expectation, which was based on the intensive management regimes typical of plantations (Table S2).

Effects of gaps on woody plant regeneration by gap characteristics

The mean effect of artificial gaps on regeneration was 10.4 times greater than for natural gaps (Fig. 1). Nearly 80% of observations for artificial gaps described positive responses to regeneration, but only 60% of observations were positive for natural gaps (Table 2). This discrepancy demonstrated that gaps formed artificially were more conducive to regeneration of woody plants.

This can be explained by one or more of three factors: 1) Natural and artificial gaps created different microsite conditions for woody plant regeneration. Natural gaps (upper gap size <1000 m^2) are usually created by windthrow or snow and cause crown damage, stem breaking or uprooting (Zhu et al. 2006). These gap makers remain on the ground in the gap where they can negatively affect the regeneration of woody plants (Clinton and Baker 2000). In contrast, artificial gaps are made by cutting target trees and leaving stumps in the ground. This causes minor soil disturbance such as trampling, and the resulting microsite conditions might be favorable to woody plant regeneration; 2) Removal of competing vegetation from artificial gaps might benefit woody plant regeneration. Liana infestation, for example, is an obstacle factor to woody plant regeneration (Toledo-Aceves and Swaine 2007) that is often removed during and following the creation of gaps (Schnitzer et al. 2004). Thus, liana densities are typically lower in artificial gaps and regenerating tree species are higher (Felton et al. 2006). Other soil preparations such as weeding after gap formation may also increase the regeneration of woody plants; 3) Differences in gap distribution patterns lead to variation in gap effects on regeneration between natural and artificial gaps. The distribution of natural gaps is more complicated than for artificial gaps because topography greatly influences natural gap formation (de Lima and de Moura 2008). For example, trees growing on ridges and slopes are more liable to be gap makers than are trees growing on flatter ground (Almquist et al. 2002). The spatial distribution of natural gaps is random, whereas anthropogenic gaps are spatially clumped (Garbarino et al. 2012). Artificial gaps are often created in sample plots with good environmental conditions rather than at randomly selected sites in a largely unmanaged forest. Runkle (1982) classified forest gaps as either canopy gaps or expanded gaps. We found that the mean effect of canopy gaps was 3.93 times greater than for expanded gaps. Yet the positive response of regeneration in canopy gaps was similar to that for expanded gaps (71% versus 65%) (Table 2). The relatively greater regeneration density in canopy gaps might be induced by the higher proportion of shade-intolerant woody plants growing in canopy gaps (15%) than in expanded gaps (4%) (Table S2). The shade-intolerant species benefitted more from the increased light availability that resulted from gap formation and regenerated at greater densities. The number of observations in canopy gaps (448) was greater than in expanded gaps (79) and this might have led to the difference in mean effect size between canopy and expanded gaps.

Table 2: Effects of gap on regeneration in response to different variables.

	Variables	Number of observations				Percentage		
		Positive	zero	Negative	Total	Positive	zero	Negative
Forest types	Natural forest	203	8	112	323	62.85	2.48	34.67
	Plantation forest	104	0	10	114	91.23	0.00	8.77
	Coniferous forest	97	0	33	130	74.62	0.00	25.38
	Coniferous-broadleaved mixed forest	112	2	32	146	76.71	1.37	21.92
	Broadleaved forest	162	7	82	251	64.54	2.79	32.67
Gap characteristics	Natural gap	136	4	89	229	59.39	1.75	38.86
	Artificial gap	235	5	58	298	78.86	1.68	19.46
	Canopy gap	320	6	122	448	71.43	1.34	27.23
	Expanded gap	51	3	25	79	64.56	3.80	31.65
	Size (m^2)	371	9	147	527	70.40	1.71	27.89
	Age (year)	115	1	52	168	68.45	0.60	30.95
Functional traits	Shade tolerant	101	1	57	159	63.52	0.63	35.85
	Intermediate	112	5	29	146	76.71	3.42	19.86
	Shade intolerant	44	0	3	47	93.62	0.00	6.38
	Evergreen coniferous	77	2	31	110	70.00	1.82	28.18
	Evergreen broadleaved	63	1	49	113	55.75	0.88	43.36
	Deciduous broadleaved	190	5	43	238	79.83	2.10	18.07
	Seedlings	168	4	69	241	69.71	1.66	28.63
	Saplings	82	5	37	124	66.13	4.03	29.84
Environmental factors	MAT (℃)	371	9	147	527	70.40	1.71	27.89
	MAP (mm)	371	9	147	527	70.40	1.71	27.89

Differences in gap size and in transition zone from understory to gap between canopy gap and expanded gap might also partially explain differences in regeneration densities. In the transition area, gap edges combine the traits of canopy gap and understory. They have greater light intensity (Brown 1996; Page and Cameron 2006) and larger growing area, i.e., the two main factors for seedling and sapling survival. All woody species appear to benefit in the transition area and can grow at higher densities than in the understory or even in the canopy gap. The edges of large gaps can positively influence plant regeneration, but negative influence may be found for small gap edges (York et al. 2003; Fahey and Puettmann 2008). Our analysis did not reflect this potential discrepancy, possibly because of the greater number of small gaps than large gaps in this study (Table S2).

Gap size is widely known as the most important gap characteristic influencing plant regeneration (Webster and Lorimer 2005; Holladay et al. 2006). However, the relationship between gap size and woody plant regeneration is interpreted differently by different researchers (Fajardo and de Graaf 2004; Arevalo and Fernandez-Palacios 2007). Our meta-analysis showed a significant and increasing trend (r = 0.114, p <0.05), i.e., the effect size increased with increasing gap size (Fig. 3a), although there were 28% and 2% observations exhibited negative or no response to the effects of gap size on regeneration density (Table 2). Gaps of <550 m^2 accounted for 93%, and gaps of <250 m^2 for 64% of the data set compiled for this meta-analysis: the relatively small gap sizes might have obscured the effect of gap size on regeneration. The magnitude of effects [*L(R)*] fluctuated widely. Nearly 68% of observations in gaps <250 m^2 documented increased regeneration densities but *L(R)* varied from -8.078 to 7.923 (Table S2). Huth and Wagner (2006) claimed that regeneration of woody plants in large gaps was inhibited by competition from herbs. Kern et al. (2012) reported that intermediate gap size, which avoided two extreme canopy conditions (large gaps and closed canopy) and provided moderate microclimate and resources, was more appropriate for regeneration and growth of tree species. Indeed, the effect of intermediate gap size on regeneration was documented in seed banks of gaps (Yan et al. 2010). Thus, the effect of gap size on regeneration may follow the "neutral theory", i.e., there exists an optimum range of gap size that promotes the regeneration of woody plants. Further studies are needed to detect the optimum range.

Gap age is another important characteristic for explaining woody plant regeneration (Burnham and Lee 2010) but accurately estimating gap age is difficult using existing methods (Richards and Hart 2011). Most observations we compiled did not present gap ages, with only 32% reporting age information (Table S2). Our meta-analysis showed a decreasing trend in magnitude of gap effect (r = -0.257, p <0.05; Fig. 3b) as gap age increased. Any differences in regeneration densities between gap and understory disappeared at gap age of about 25 years. This is because gap size declines with increasing age due to refilling of gaps by surrounding trees and regeneration within gaps. Twenty-five years is long enough for most trees to grow to heights where they can create shade similar to that of the overstory even without reaching canopy tree height (Richards and Hart 2011). We found that gaps aged ≥30 years exhibited regeneration as low as to be regarded as regeneration failure. Seed source shortage or repeated negative disturbance may account for this phenomenon.

Effects of gaps on woody plant regeneration by plant functional type

Shade tolerance of woody plants is one of the focuses of gap regeneration research (Denslow 1980; Gravel et al. 2010). Many studies addressed the relationship between shade tolerance and gap size, but the reported results remain controversial (Kern et al. 2012). According to the Gap Partitioning Hypothesis (Denslow 1980), shade-intolerant species perform best in large gaps, but small gaps and intact forest provide better habitat for shade-tolerant species. However, the definitions of "large" and "small" are so ambiguous among researches that it is difficult to delimit a range for gap size without overlapping woody plants of differing shade tolerance. We compared the regeneration of different shade-tolerance species in forest gaps and understory without considering gap size. On average, the density of shade-intolerant species in gaps was 24.75 times higher than that in understory (Fig. 4). This exceeded our expectation although the positive trend is consistent with most individual studies (94% of observations of intolerant species exhibited positive responses; Table 2) (Dickinson et al. 2000). Shade-tolerant species exhibited a positive effect (+124%, 95% CI: 48-241%) on average even though 36% of observations of tolerant species showed negative responses (Table 2). This positive response of tolerant species seemed to be different from some traditional opinions following the Gap Partitioning Hypothesis (Holladay et al. 2006). Although higher light intensity after gap formation might negatively influence the survival and growth of shade-tolerant woody plants, sufficient growing space seemed to offset, or even outweighed this disadvantage. Shade tolerant species probably make a trade-off among various factors for better survival (Poorter 2009).

Leaf morphology reflects some differences in physiological features of woody plants, and influences woody plant regeneration (Kamiyama et al. 2010). The effect of gaps on regeneration of deciduous broadleaved species was 2.30 and 3.12 times more than on evergreen coniferous and evergreen broadleaved species, respectively (Fig. 1). But the difference between evergreen coniferous and evergreen broadleaved species was not significant (Fig. 1). The more pronounced effect of deciduous woody plants may be partially due to shade tolerance of regenerated species. Deciduous species are usually shade-intolerant or intermediate (accounting for 75% of the compiled observations), and they regenerated aggressively in gaps. In contrast, shade-tolerant species accounted for a larger proportion of conifers (81%), and regenerated at lower densities in gaps (Sakai and Ohsawa 1993). Although the percentage of shade-intolerant species in our meta-analysis was similar between deciduous and evergreen species (13% versus 11%), the percentage of shade-tolerant species among deciduous species (25%) was far lower than among evergreen species (69%) (Table S2). This might also have led to higher regeneration density for deciduous species. In addition, regeneration of some evergreen species was less dependent on gaps.

No significant difference of gap effects on regeneration was found in responses to seedlings and saplings. This might have resulted from the typically short study durations that masked difference between survival of seedlings and saplings. In addition, classification criteria for seedling versus sapling varied by various studies (Dobrowolska 2006; Bolton and D'Amato 2011). Standardized definition of seedlings and saplings and long-term monitoring in future would contribute to better understanding of the effects of gaps on regeneration of seedlings and saplings.

Dependence of gap regeneration on ambient temperature and precipitation

With increasing MAT and MAP, the magnitude of gap effect *Ln(R)* declined (Fig. 5a, b). The significant positive correlation ($r = 0.520$, $p < 0.05$; Fig. 6) between MAT and MAP implied that heat and moisture varied synchronously. Generally, temperature and precipitation or heat and moisture conditions determine the distribution and growth of woody plants (Schliemann and Bockheim 2011). When temperature and precipitation are low, i.e., heat and moisture are limiting factors for woody plant regeneration, gaps promote woody plant regeneration because gaps can improve the water and thermal environments by opening the canopy and relieving the impacts of canopy closure on decreasing the availability of heat and moisture. The difference in regeneration density between gaps and understory was greater when temperature and precipitation were lower. In contrast, as temperature and precipitation increased, i.e., the limiting effects of heat and moisture resources declined, the conducive effect of gaps on woody plant regeneration also declined, eventually leading to reduced response to regeneration. The decreasing trend of the gap effect on woody plant regeneration along MAT and MAP gradients suggests that positive responses of woody plants to gap regeneration decline or disappear in areas where reproduction of woody species is not limited by temperature and precipitation.

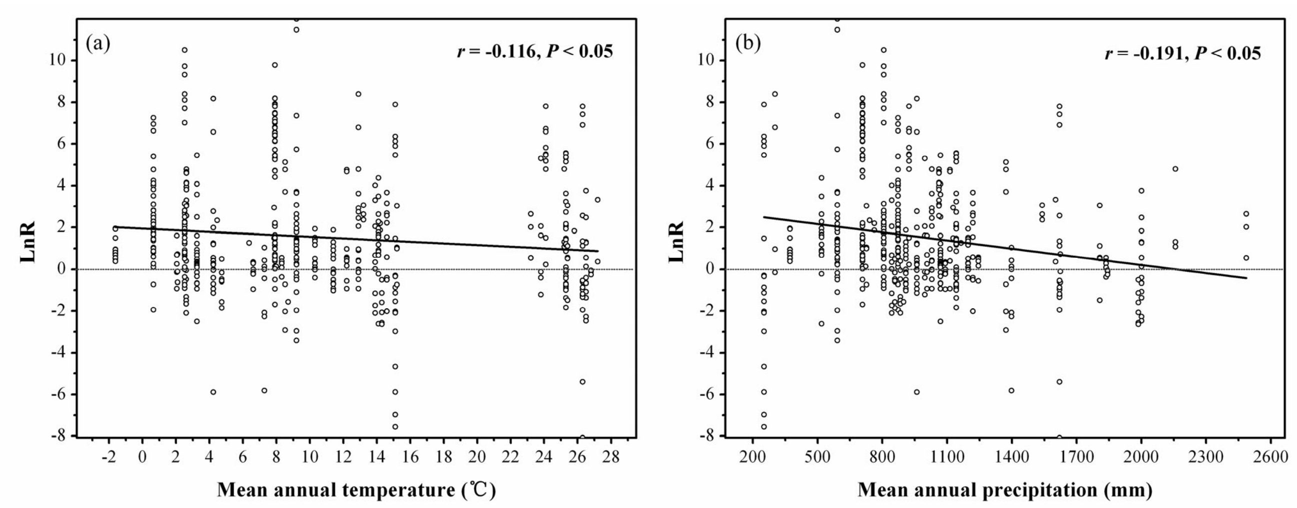

Fig. 5: The effects of environmental factors (mean annual temperature and mean annual precipitation, numbers of observations = 527) on woody plant regeneration. *Ln(R)* = 0 means no difference in regeneration density between gaps and understory. Regression lines, Pearson correlations (r), and significance level (P) are indicated on the figure.

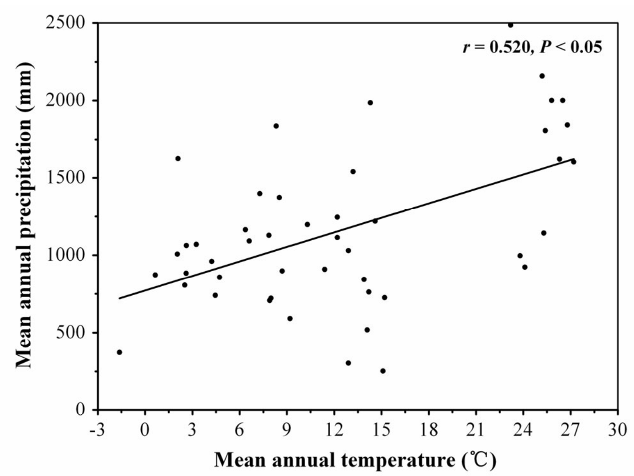

Fig. 6: Relationship between mean annual temperature and mean annual precipitation of all studies (47 locations from 42 publications) included in the current meta-analysis. Regression line, Pearson correlation (r), and significance level (P) are indicated on the figure.

Conclusions and implications

Even though many studies evaluated the effects of forest gaps on regeneration from almost all aspects (Kuuluvainen and Juntunen 1998; van der Meer et al. 1998; Drobyshev 1999; Schulze 2008; Lara-Gonzalez et al. 2009; Fahey and Lorimer 2013; Lawson and Michler 2014), this meta-analysis provided quantitative evidence to confirm the large effect of gaps on increasing regeneration by woody species, i.e., gaps increased woody plant regeneration by an average of 359%. The magnitudes of positive effects of gaps on woody plant regeneration are determined by forest types, gap characteristics, plant functional traits and site conditions. Gaps in plantation forests exhibited the most pronounced effect on woody plant regeneration. Artificial gaps also showed greater advantage over other gap types due to human disturbances. The significantly higher positive regeneration responses in gaps of plantation forests or in artificial gaps revealed in this study (Fig. 2) could support the suggestion that gap disturbance is a key metric for forest management (Mason and Zhu 2014). Regenera-

tion density decreased with both gap size and gap age because gap size decreased with increasing gap age. Furthermore, shade tolerance weighted more in accounting for regeneration differences between forest gaps and understory compared with other plant functions such as leaf morphological traits or growth stage. Shade-tolerant woody plants also benefit from forest gaps, although the effects are less pronounced than for shade-intolerant species. The declining trend of gap effect on woody plant regeneration along MAT and MAP gradients might imply that gap regeneration is more effective in lower temperature and precipitation conditions.

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References

Almquist BE, Jack SB, Messina MG. 2002. Variation of the treefall gap regime in a bottomland hardwood forest: relationships with microtopography. *Forest Ecology and Management*, **157**: 155−163.

Arevalo JR, Fernandez-Palacios JM. 2007. Treefall gaps and regeneration composition in the laurel forest of Anaga (Tenerife): a matter of size? *Plant Ecology*, **188**: 133−143.

Bai E, Li S, Xu W, Li W, Dai W, Jiang P. 2013. A meta - analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytologist*. **199**: 441−451.

Bolton NW, D'Amato AW. 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. *Forest Ecology and Management*, **262**: 1215−1222.

Brokaw NV. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica*, **14**: 158−160.

Brown N. 1996. A gradient of seedling growth from the centre of a tropical rain forest canopy gap. *Forest Ecology and Management*, **82**: 239−244.

Burnham KM, Lee TD. 2010. Canopy gaps facilitate establishment, growth, and reproduction of invasive *Frangula alnus* in a *Tsuga canadensis* dominated forest. *Biological Invasions*, **12**: 1509−1520.

Clarke PJ. 2004. Effects of experimental canopy gaps on mangrove recruitment: lack of habitat partitioning may explain stand dominance. *Journal of Ecology*, **92**: 203-213.

Clinton BD, Baker CR. 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. *Forest Ecology and Management*, **126**: 51−60.

de Lima RAF, de Moura LC. 2008. Gap disturbance regime and composition in the Atlantic Montane Rain Forest: the influence of topography. *Plant Ecology*, **197**: 239−253.

Denslow JS. 1980. Gap partitioning among tropical rainforest trees. *Biotropica*, **12**: 47−55.

Dickinson MB, Whigham DF, Hermann SM. 2000. Tree regeneration in felling and natural treefall disturbances in a semideciduous tropical forest in Mexico. *Forest Ecology and Management*, **134**: 137−151.

Dobrowolska D. 2006. Oak natural regeneration and conversion processes in mixed Scots pine stands. *Forestry*, **79**: 503−513.

Drobyshev IV. 1999. Regeneration of Norway spruce in canopy gaps in *Sphagnum-Myrtillus* old-growth forests. *Forest Ecology and Management*, **115**: 71−83.

Duguid MC, Ashton MS. 2013. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. *Forest Ecology and Management*, **303**: 81−90.

Elias RB, Dias E. 2009. Gap dynamics and regeneration strategies in *Juniperus-Laurus* forests of the Azores Islands. *Plant Ecology*, **200**: 179−189.

Fahey RT, Lorimer CG. 2013. Restoring a midtolerant pine species as a component of late-successional forests: Results of gap-based planting trials. *Forest Ecology and Management*, **292**: 139−149.

Fahey RT, Puettmann KJ. 2008. Patterns in spatial extent of gap influence on understory plant communities. *Forest Ecology and Management*, **255**: 2801−2810.

Fajardo A, de Graaf R. 2004. Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in Southern Chile. *Plant Ecology*, **173**: 95−105.

Felton A, Felton AM, Wood J, Lindenmayer DB. 2006. Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest. *Forest Ecology and Management*, **235**: 186−193.

Galhidy L, Mihok B, Hagyo A, Rajkai K, Standovar T. 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecology*, **183**: 133−145.

Garbarino M, Mondino EB, Lingua E, Nagel TA, Dukic V, Govedar Z, Motta R. 2012. Gap disturbances and regeneration patterns in a Bosnian old-growth forest: a multispectral remote sensing and ground-based approach. *Annals of Forest Science*, **69**: 617−625.

Gravel D, Canham CD, Beaudet M, Messier C. 2010. Shade tolerance, canopy gaps and mechanisims of coexistence of forest trees. *Oikos*, **119**: 475−484.

Gurevitch J, Hedges LV. 1999. Statistical issues in ecological meta-analyses. *Ecology*, **80**: 1142−1149.

He ZS, Liu JF, Wu CT, Zheng SQ, Hong W, Su SJ, Wu CZ. 2012. Effects of forest gaps on some microclimate variables in *Castanopsis kawakamii* natural forest. *Journal of Mountain Science*, **9**: 706−714.

Hedges LV, Gurevitch J, Curtis PS. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**: 1150−1156.

Holladay C-A, Kwit C, Collins B. 2006. Woody regeneration in and around aging southern bottomland hardwood forest gaps: effects of herbivory and gap size. *Forest Ecology and Management*, **223**: 218−225.

Hutchinson TF, Long RP, Rebbeck J, Sutherland EK, Yaussy DA. 2012. Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. *Canadian Journal of Forest Research*, **42**: 303−314.

Huth F, Wagner S. 2006. Gap structure and establishment of Silver birch regeneration (*Betula pendula* Roth.) in Norway spruce stands (*Picea abies* L. Karst.). *Forest Ecology and Management*, **229**: 314−324.

Ibanez I, McCarthy-Neumann S. 2014. Integrated assessment of the direct and indirect effects of resource gradients on tree species recruitment. *Ecology*, **95**: 364−375.

Johnson DW, Curtis PS. 2001. Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management*, **140**: 227−238.

Kamiyama C, Oikawa S, Kubo T, Hikosaka K. 2010. Light interception in species with different functional groups coexisting in moorland plant communities. *Oecologia*, **164**: 591−599.

Kern CC, Reich PB, Montgomery RA, Strong TF. 2012. Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings?

Forest Ecology and Management, **267**: 134–143.

Kuuluvainen T, Juntunen P. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal *Pinus sylvestris* forest. *Journal of Vegetation Science*, **9**: 551–562.

Lawson SS, Michler CH. 2014. Afforestation, restoration and regeneration - Not all trees are created equal. *Journal of Forestry Research*, **25**(1): 3–20.

Lara-Gonzalez R, Sanchez-Velasquez LR, Corral-Aguirre J. 2009. Regeneration of *Abies religiosa* in canopy gaps versus understory, Cofre de Perote National Park, Mexico. *Agrociencia*, **43**: 739–747.

Lee CS, Kim JH, Yi H, You YH. 2004. Seedling establishment and regeneration of Korean red pine (*Pinus densiflora* S. et Z.) forests in Korea in relation to soil moisture. *Forest Ecology and Management*, **199**: 423–432.

Leithead M, Silva LCR, Anand M. 2012. Recruitment patterns and northward tree migration through gap dynamics in an old-growth white pine forest in northern Ontario. *Plant Ecology*, **213**: 1699–1714.

Lin D, Xia J, Wan S. 2010. Climate warming and biomass accumulation of terrestrial plants: a meta - analysis. *New Phytologist*, **188**: 187–198.

Long JN. 2009. Emulating natural disturbance regimes as a basis for forest management: A North American view. *Forest Ecology and Management*, **257**: 1868–1873.

Lu ZH, Wu G, Ma X, Bai GX. 2002. Current situation of Chinese forestry tactics and strategy of sustainable development. *Journal of Forestry Research*, **13**: 319-322.

Madsen P, Hahn K. 2008. Natural regeneration in a beech-dominated forest managed by close-to-nature principles-a gap cutting based experiment. *Canadian Journal of Forest Research*, **38**: 1716–1729.

Mallik AU, Kreutzweiser DP, Spalvieri CM. 2014. Forest regeneration in gaps seven years after partial harvesting in riparian buffers of boreal mixedwood streams. *Forest Ecology and Management*, **312**: 117–128.

Marthews TR, Burslem DF, Phillips RT, Mullins CE. 2008. Modelling direct radiation and canopy gap regimes in tropical forests. *Biotropica*, **40**: 676–685.

Mason W. 2003. Continuous cover forestry: developing a close-to-nature forest management in conifer plantations in upland Britain. *Scottish Forestry*, **57**: 141–150.

Mason W, Zhu J. 2014. Silviculture of planted forests managed for multi-functional objectives: lessons from Chinese and British experiences. *In*: T. Fenning (ed), *Challenges and Opportunities for the World's Forests in the 21st Century*. New York: Springer, pp. 37–54.

Mizunaga H. 2007. Do finer gap mosaics provide a wider niche for *Quercus gilva* in young Japanese cedar plantations than coarser mosaics? Simulation of spatial heterogeneity of light availability and photosynthetic potential. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **37**: 1545–1553.

Muscolo A, Sidari M, Mercurio R. 2007. Influence of gap size on organic matter decomposition, microbial biomass and nutrient cycle in Calabrian pine (*Pinus laricio*, Poiret) stands. *Forest Ecology and Management*, **242**: 412–418.

Nagel TA, Svoboda M, Rugani T, Diaci J. 2010. Gap regeneration and replacement patterns in an old-growth *Fagus-Abies* forest of Bosnia-Herzegovina. *Plant Ecology*, **208**: 307–318.

Nuske RS, Sprauer S, Saborowski J. 2009. Adapting the pair-correlation function for analysing the spatial distribution of canopy gaps. *Forest Ecology and Management*, **259**: 107–116.

Page LM, Cameron AD. 2006. Regeneration dynamics of Sitka spruce in artificially created forest gaps. *Forest Ecology and Management*, **221**: 260–266.

Paquette A, Bouchard A, Cogliastro A. 2006. Survival and growth of under-planted trees: a meta-analysis across four biomes. *Ecological Applications*, **16**: 1575–1589.

Poorter L. 2009. Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *New Phytologist*, **181**: 890–900.

Richards JD, Hart JL. 2011. Canopy gap dynamics and development patterns in secondary *Quercus* stands on the Cumberland Plateau, Alabama, USA. *Forest Ecology and Management*, **262**: 2229–2239.

Rosenberg MS, Adams DC, Gurevitch J. 2000. MetaWin: statistical software for meta-analysis. Sinauer Associates Sunderland, Massachusetts, USA.

Runkle JR. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology*, **63**: 1533–1546.

Sakai A, Ohsawa M. 1993. Vegetation pattern and microtopography on a landslide scar of Mt Kiyosumi, central Japan. *Ecological Research*, **8**: 47–56.

Schliemann SA, Bockheim JG. 2011. Methods for studying treefall gaps: a review. *Forest Ecology and Management*, **261**: 1143–1151.

Schnitzer SA, Parren MP, Bongers F. 2004. Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon. *Forest Ecology and Management*, **190**: 87–98.

Schulze M. 2008. Technical and financial analysis of enrichment planting in logging gaps as a potential component of forest management in the eastern Amazon. *Forest Ecology and Management*, **255**: 866–879.

Toledo-Aceves T, Swaine MD. 2007. Effect of three species of climber on the performance of *Ceiba pentandra* seedlings in gaps in a tropical forest in Ghana. *Journal of Tropical Ecology*, **23**: 45–52.

van der Meer PJ, Sterck FJ, Bongers F. 1998. Tree seedling performance in canopy gaps in a tropical rain forest at Nouragues, French Guiana. *Journal of Tropical Ecology*, **14**: 119–137.

Wang GL, Liu F. 2011. The influence of gap creation on the regeneration of *Pinus tabuliformis* planted forest and its role in the near-natural cultivation strategy for planted forest management. *Forest Ecology and Management*, **262**: 413–423.

Watt AS. 1947. Pattern and process in the plant community. *Journal of Ecology*, **35**: 1-22.

Webster CR, Lorimer CG. 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. *Ecological Applications*, **15**: 1245–1262.

Whitmore T. 1989. Canopy gaps and the two major groups of forest trees. *Ecology*, **70**: 536–538.

Yamamoto SI. 1992. The gap theory in forest dynamics. *Botanical Magazine-Tokyo*, **105**: 375–383.

Yan QL, Zhu JJ, Zhang JP, Yu LZ, Hu ZB. 2010. Spatial distribution pattern of soil seed bank in canopy gaps of various sizes in temperate secondary forests, Northeast China. *Plant and Soil*, **329**: 469–480.

York RA, Battles JJ, Heald RC. 2003. Edge effects in mixed conifer group selection openings: tree height response to resource gradients. *Forest Ecology and Management*, **179**: 107–121.

Zhang C, Zou CJ, Peltola H, Wang KY, Xu WD. 2013. The effects of gap size and age on natural regeneration of *Picea mongolica* in the semi-arid region of Northern China. *New Forests*, **44**: 297–310.

Zhu JJ, Li XF, Liu ZG, Cao W, Gonda Y, Matsuzaki T. 2006. Factors affecting the snow and wind induced damage of a montane secondary forest in northeastern China. *Silva Fennica*, **40**: 37–51.

Zhu JJ, Matsuzaki T, Lee FQ, Gonda Y. 2003. Effect of gap size created by thinning on seedling emergency, survival and establishment in a coastal pine forest. *Forest Ecology and Management*, **182**: 339–354.